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## Forum

### Nutritional thermal ecology: investigating the combined influence of temperature and nutrient availability on plant-ectotherm trophic interactions

Cédric L. Meunier<sup>1</sup>✉, Inga V. Kirstein<sup>1</sup>, Felix Weber<sup>1</sup>, Ann Marielle Evarita<sup>1</sup>, Cecilia Laspoumaderes<sup>2</sup> and Maarten Boersma<sup>1,3</sup>

<sup>1</sup>Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Helgoland, Germany

<sup>2</sup>Departamento de Ecología, Laboratorio de Limnología, INIBIOMA, CONICET-Universidad Nacional del Comahue, Bariloche, Argentina

<sup>3</sup>University of Bremen, Germany

Correspondence: Cédric L. Meunier ([cedric.meunier@awi.de](mailto:cedric.meunier@awi.de))

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Many primary consumers in freshwater, marine and terrestrial systems are ectotherms (e.g. zooplankton and insects), whose metabolisms, and therefore nutritional demands, are modulated by temperature. Further, nutrient availability largely influences the quality of resources consumed by these organisms, and hence affects whether nutritional demands of consumers are fulfilled. From these considerations, a crucial question arises: how do temperature and nutrient availability together modulate trophodynamics at the basis of food webs? Addressing this question for zooplankton and insects is essential since these consumers are the most abundant metazoans on Earth, and they link primary production to higher trophic levels. Here, we synthesize the existing literature and offer avenues to guide future scientific endeavours. We highlight that the vast majority of studies on the combined influence of temperature and nutrient availability published to date focus on at least one of the following research topics: 1) metabolic requirements of ectotherms; 2) feeding behaviour; 3) eco-evolutionary processes; and 4) trophodynamics. We pose that further advances in this field of research may provide a robust understanding of how modulations of consumer metabolic requirements and resource quality define consumer–producer interactions across marine, freshwater and terrestrial ecosystems. This research effort would enable to combine the fields of Ecological stoichiometry and of Metabolic theory of ecology, and create an integrated approach, which we propose to call Nutritional thermal ecology.

Keywords: Ecological stoichiometry, invertebrates, metabolic theory of ecology, nutritional geometry, trophic interactions



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## Resource quality, consumer nutritional demands, and their drivers

In food webs, the quality of a given trophic level (resource) for the subsequent one (consumer) is a key determinant for the transfer of energy and material from one trophic level to the next, and consequently of community structure and function (Ruess and Müller-Navarra 2019, Schmitz and Leroux 2020). Elemental composition of the food (including macronutrients such as carbon, nitrogen, phosphorus, on which we will focus here) is a key feature determining resource quality, as it drives consumers' performance and subsequently controls trophic dynamics (Simpson and Raubenheimer 2012, Hessen et al. 2013, Sperfeld et al. 2017, Ruess and Müller-Navarra 2019, Meunier et al. 2023). Given the ecological consequences of nutritional imbalances and limitations for population and community dynamics of heterotrophs, it is no surprise that identifying the conditions under which animal consumers experience nutritional deficiencies in their food resources has been, and still remains, a major research topic in marine, freshwater and terrestrial ecology (Buchkowski et al. 2019, Schiettekatte et al. 2020, Hamann et al. 2021). This is particularly timely because human activities have altered, and will continue to alter, biogeochemical cycles and, in turn, the nutritional value of resources across ecosystems (Peñuelas et al. 2013, Ibáñez et al. 2023, Peñuelas and Sardans 2023).

Alterations of resource quality at the base of food webs may also affect higher trophic levels (Peñuelas et al. 2013, Meunier et al. 2016a, Teurlincx et al. 2017), as signals of nutritional imbalances are transferred up the food chain (Malzahn et al. 2007, Boersma et al. 2008). This sensitivity to nutritional imbalances is influenced by consumers' metabolic requirements, which are not static, and temperature is arguably the environmental driver influencing metabolism most. As posed by the framework of the metabolic theory of ecology, temperature is a master variable that controls biological activity through its fundamental effects on metabolic rates (Brown et al. 2004, Burger et al. 2019, 2021). Indeed, metabolic rate sets the pace of life by determining the overall rate at which organisms take up energy and nutrients, and subsequently convert and allocate them to growth and reproduction processes. The fields of ecological stoichiometry (Sternner and Elser 2002) and of nutritional geometry (Simpson and Raubenheimer 2012) have a long history of studying the effects of multiple elements and their ratios on consumer performance, but have only recently started dealing with the interactions between stoichiometric dietary needs and temperature.

Given the over-riding importance of temperature on metabolic rates of ectotherms, understanding these interactions is critical, particularly in the light of global warming. Simultaneous shifts in resource quality and in the nutritional requirements of ectotherm consumers may modulate nutritional interactions between consumers and their resources, and influence match-mismatch conditions, potentially causing changes in community structure, and drive biodiversity

(Binzer et al. 2016, O'Gorman et al. 2019, Chase et al. 2020, Eastwood et al. 2022, Yamamichi et al. 2023). Hence, studies on the combined influence of nutrient availability and temperature on trophic interactions between ectotherm primary consumers and their resources are key to understand and assess food web stability. This topic has gained prominence in the scientific literature in recent years (Cross et al. 2015, Ruiz et al. 2020, Zhang et al. 2020a, Laspoumaderes et al. 2022, Zhu et al. 2023), and a synthesis of the current knowledge is needed to identify commonalities (and possibly differences) between marine, freshwater, and terrestrial systems, and to guide future research.

## Interactions between autotrophs and ectotherm herbivores across ecosystems

A strong case can be made that resource quality and metabolic requirements of ectotherms may interact similarly in marine, freshwater, and terrestrial systems. On the one hand, many aquatic and terrestrial primary producers do not regulate their elemental composition (Sternner and Elser 2002, Meunier et al. 2014, Letscher et al. 2023). Hence, while the elemental composition of primary producers can be influenced by temperature (Yvon-Durocher et al. 2017, Lie et al. 2022), the availability of nutrients is the main environmental driver determining their elemental composition, and thereby their quality as resource for primary consumers (Elser et al. 2010, Zhang et al. 2020b, Sauterey and Ward 2022). On the other hand, the metabolic rates of all ectotherms increase with temperature (Brown et al. 2004, Burger et al. 2019, 2021), and, consequently, the metabolic requirements in marine, freshwater, and terrestrial ectotherm primary consumers may be similarly influenced by temperature. Interestingly, the metabolic requirements for different elements, such as carbon (C), nitrogen (N), and phosphorus (P), may have different temperature dependencies, and as a result the relative requirements for these different nutrients may change over a temperature gradient. However, cross-system comparisons are rare, which limits our ability to define overarching ecological rules (Gibert 2019, Mestre et al. 2022).

Exploring potential cross-system commonalities in processes driving resource quality and consumer dietary requirements offers a unique chance to identify these fundamental ecological principles. Recent advances in ecological stoichiometry, nutritional geometry, and metabolic ecology offer a promising base to develop a synthetic framework to quantitatively assess how temperature and nutrients interact to control ecological dynamics (Allen and Gillooly 2009, Kim et al. 2020, Zhang et al. 2020a, El-Sabaawi et al. 2023). Controlled laboratory experiments (Boersma et al. 2016, Kim et al. 2020, Laspoumaderes et al. 2022), but also mechanistic models (Damos et al. 2011, Anderson et al. 2017, Ruiz et al. 2020), and studies of populations across environmental gradients (González-Bergonzoni et al. 2012, Sinclair et al. 2012, Gibert 2019) have enabled physiologists and ecologists to examine temperature–nutrient interactions.

More recent developments, such as threshold elemental ratio (TER) models (Cross et al. 2015, Laspoumaderes et al. 2022, Meunier et al. 2023), explicitly blend both metabolic and stoichiometric frameworks and have helped to further bridge the commonly disparate perspectives of energy and nutrients in ecology. Together, results from these studies hold great promise for advancing our understanding of how temperature and nutrients interact to affect trophodynamics. Although an increasing number of studies have begun to examine temperature–nutrient interactions (Makino et al. 2011, Ruiz et al. 2020, Zhang et al. 2020a, b, Laspoumaderes et al. 2022), a conceptual synthesis is needed to identify key concepts and emerging patterns, and to highlight productive areas for future research. We consider that studies on the combined influences of temperature and nutrient availability on trophodynamics may allow us to apply modern ecological theory toward solving important environmental issues (Thrall and Blanc 2023). In addition, progress in this area has great potential to improve our understanding of how environmental effects on individuals scale up to influence whole-ecosystem dynamics (Cross et al. 2015).

## Nutritional thermal ecology

The vast majority of studies on the combined influence of temperature and nutrient availability published to date focus on at least one of the following research topics: 1) metabolic

requirements of ectotherms; 2) feeding behaviour; 3) eco-evolutionary processes; and 4) trophodynamics (Fig. 1). We propose that future studies should continue to investigate research questions 1–3 by conducting experiments and field surveys addressing the impact of temperature and nutrient conditions on key aquatic and terrestrial ectotherm primary consumers. These invaluable data on the parameters driving trophic interactions at the basis of food webs could be integrated in trophodynamics models to address research question 4. Altogether, this work may enable the scientific community to identify overarching ecological rules on the influence of temperature and nutrient availability on trophodynamics across ecosystems. This research effort would enable to combine the fields of Ecological stoichiometry and of Metabolic theory of ecology, and create an integrated approach, which we propose to call ‘Nutritional thermal ecology’. In the following, we highlight recent results from the literature for each research topic, and we suggest avenues for future research in Nutritional thermal ecology.

### Metabolic requirements of ectotherms

Metabolic requirements of ectotherm consumers are not static, they are largely influenced by environmental temperature. For instance, Rho and Lee (2017) identified that the interplay between temperature and resource quality mediates phenotypic variations in growth rates and energy utilization in the insect *Tenebrio molitor*, the yellow mealworm beetle. A

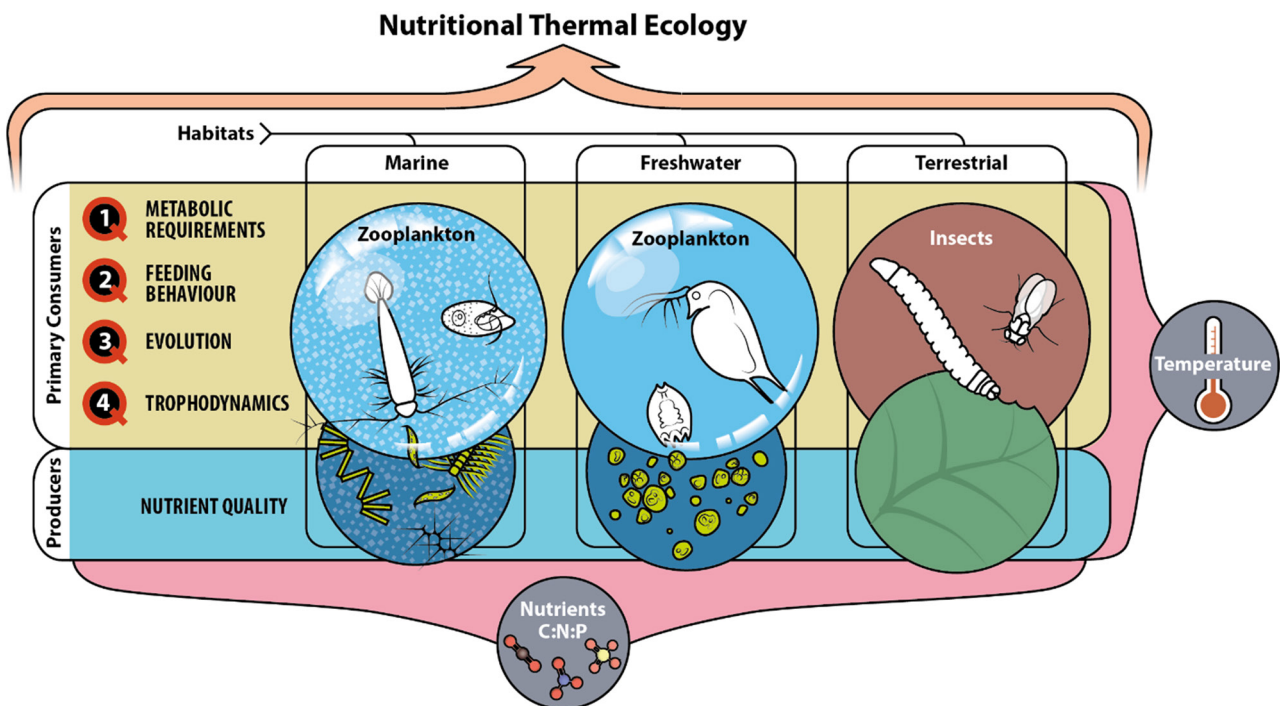


Figure 1. Schematic overview of research areas which address the influence of temperature and nutrient availability on producer–consumer interactions in marine, freshwater and terrestrial systems. We synthesize them around four topics, namely 1) metabolic requirements of ectotherms; 2) feeding behaviour; 3) eco-evolutionary processes; and 4) trophodynamics, which may lead to an integrated approach we propose to call Nutritional thermal ecology.

straightforward way to assess temperature–food quality interactions is to investigate temperature effects on the threshold elemental ratio (TER) (Frost et al. 2006, Cross et al. 2015, Laspoumaderes et al. 2022, Meunier et al. 2023). The  $TER_{C:X}$  is the carbon:nutrient (C:X) ratio in the food that exactly matches the current physiological requirements for metabolism and resulting growth and reproduction of the consumer, with hence neither C nor X being limiting or in excess. The TER is a quantitative tool that integrates multiple responses of organism biochemistry and physiology. A low  $TER_{C:X}$  indicates higher needs for the nutrient X relative to C, while a higher  $TER_{C:X}$  indicates the opposite. Cross et al. (2015) noted that there were few studies on how temperature affects the TER and made a strong case to measure the  $TER_{C:X}$  at different temperatures. Following this approach, recent results show that the nutritional requirements of zooplankton, and the resource quality which maximizes the growth of these ectotherms, are not constant but rather vary with temperature (Persson et al. 2011, Boersma et al. 2016, Berlinghof 2020, Ruiz et al. 2020, Laspoumaderes et al. 2022). These results suggest that variations in metabolic demands in ectotherms with temperature on the one hand, and variations in resource quality with nutrient availability on the other hand, may modulate nutritional match-mismatch situations (Table 1). As an attempt to unify the rather disparate results from existing studies, Laspoumaderes et al. (2022) published a concept for zooplankton based on the observation that the TER is not constant, but varies with temperature. Their work suggest that, when temperature increases from cold to intermediate, the demand of C relative to nutrients increases as a result of increasing respiration rates and nutrient use efficiency, until the maximum value of the  $TER_{C:X}$  is reached. When temperatures exceed the normal thermal environment of the organism, demands of nutrients relative to C may increase as a result of reduced nutrient use efficiency (Table 1). Lastly, C demands relative to nutrient may increase when temperature is excessive which may reflect the physiological stress that amplifies C-demands for respiratory and catabolic processes (Schmitz 2013, Ye et al. 2019,

Moreno et al. 2020, Leles and Levine 2023). These were fairly ad hoc explanations, and contradict to some extent the modelling outcomes of Anderson et al. (2017) who predicted no change of TER with temperature, assuming that all anabolic and catabolic processes scale with temperature in a similar way. Most importantly, studies exploring broad these thermal ranges and appropriate gradients of resource C:X ratios are rare, and more efforts in this direction are needed to assess potential cross-system commonalities, as they offer a unique chance to identify core ecological tenets (Table 1). In addition to TER, the stoichiometric mismatch between consumers and nutrients in their food can also be quantified by trophic stoichiometric ratios (TSRs) (Filipiak and Filipiak 2022). The TSR is a useful tool to identify scarce elements in food sources which influence the fitness of consumers (Filipiak and Weiner 2017, Zhang et al. 2024). While the field of ecological stoichiometry has shown that food C:N:P ratios are important indicators for the growth and population size of organisms (Zhang et al. 2023), other nutritional elements such as sodium, calcium, copper and zinc may also have significant impacts on consumers (Filipiak et al. 2016, Filipiak and Weiner 2017). Hence, the TSR not only serves as a measure of resource quality, it is also an effective tool for predicting the growth, development and feeding strategies of invertebrates, as well as the decomposition rate and primary productivity of ecosystems (Filipiak and Filipiak 2022, Zhang et al. 2024). Since these patterns are anchored in physiological responses of ectotherms to temperature, we suggest that they may apply to ectotherm primary consumers across systems, from marine zooplankton, to freshwater zooplankton, to terrestrial insects.

### Feeding behaviour

There are several pre- (Grunseich et al. 2019, Koehl 2019, Santangelo et al. 2019) and post-ingestion (Simpson and Raubenheimer 2012, Bertić et al. 2023) mechanisms allowing primary consumers to handle nutrient imbalances in their food, and to achieve a balanced nutrition even when

Table 1. Overview of the hypotheses, predictions, and how these could be tested through different study types within Nutritional thermal ecology.

Hypothesis	Prediction	Study type
Temperature modulates the balance between energy and nutrient demands in ectotherms	Demands for nutrients relative to energy increase below and above ambient temperatures	Experiments testing the influence of gradients of resource quality on consumer fitness along broad thermal ranges, using TER or TSR as metrics.
Temperature modulates the feeding preferences of ectotherms	Shifts in top–down pressure with temperature influence prey populations	Determining the diet composition of ectotherms along temperature gradients through feeding experiments, stable isotope studies, or gut content analyses. Quantification of top–down pressure on different prey types.
Ectotherms may acclimate or adapt to suboptimal temperature and resource quality	Metabolic nutritional demands of ectotherms shift in response to long-term exposure to different temperatures and resource qualities	Long-term eco-evolutionary studies testing different temperatures and resource qualities, combined with common garden experiments.
Temperature and resource quality modulate interaction strengths between low trophic levels	Shifts in interaction strength at low trophic levels cascade to higher trophic levels and destabilize food webs	Incorporate data from the above-mentioned studies into food web models to quantify the influence of warming and resource quality on the structure, level of organization, and network interactions of food webs.



food quality is suboptimal (Deans et al. 2022, Meunier et al. 2023). To reduce metabolic costs and to avoid deleterious effects of constituents taken up in excess (Zhou and Declerck 2019, 2021), pre-ingestion mechanisms such as selective feeding are of considerable importance (Meunier et al. 2023). Selective feeding on the basis of nutritional quality has been fairly well described for terrestrial (Behmer 2009, Simpson and Raubenheimer 2012), and for aquatic primary consumers (Meunier et al. 2018, Koehl 2019). Since many zooplankton and insect species can adjust the quality of their diet through selective feeding (Meunier et al. 2012, 2016b, Simpson and Raubenheimer 2012), temperature, through its influence on the metabolic requirements of primary ectotherm consumers, could modulate the top-down pressure exerted by these consumers on specific prey taxa (Table 1). Indeed, consumers affect their environment not only by the selective retention of scarce elements and the excretion of abundant elements (Meunier et al. 2018, Daufresne 2021, Karakuş et al. 2022, Peller et al. 2022), but also by selective feeding, i.e. removal of targeted resources. Warming might increase herbivory in aquatic ectotherm omnivores (Floeter et al. 2005, González-Bergonzoni et al. 2012, Boersma et al. 2016), but there is still no study that explored the consequences of this dietary shift for the abundance or diversity of primary producers (Table 1). Similarly, to the best of our knowledge, studies on the impact of warming through increased herbivory by omnivores are lacking in terrestrial ecosystems (Zhang et al. 2020b). Since selective feeding can have profound consequences for nutrient fluxes (Kagata and Ohgushi 2011) and for the stability of consumer and resource populations (Landi et al. 2018), it is crucial to close this knowledge gap to gain deeper understanding of aquatic and terrestrial food web processes. Therefore, more work that tests the effects of temperature on the feeding preferences of ectotherm consumers is needed.

### Eco-evolutionary processes

Physiological and behavioural responses to nutritional mismatches may not be linear, and rapid adaptation responses towards temperature and resource quality changes need to be considered (de Amorim et al. 2023, de Juan et al. 2023, deMayo et al. 2023, Yamamichi et al. 2023). Traditionally, evolution has been considered to be a much slower process than ecological dynamics but recent studies, have found that evolution can be rapid enough to affect ecological processes (Bitter et al. 2021, Rodríguez-Verdugo and Ackermann 2021, Loreau et al. 2022). Physiological stress resulting from nutrient limitation and suboptimal temperature can affect eco-evolutionary dynamics in multiple ways (Bitter et al. 2021), by altering the strength of selection, the response to selection for ecologically relevant organismal characteristics, and by directly altering population dynamics which in turn feeds back onto evolution. Species may acclimate or adapt to suboptimal temperature and nutrient supply conditions, which may be critical for determining how individuals respond to various environmental constraints (Table 1). However, to the best of our knowledge, only very few studies to date

have directly focused on these eco-evolutionary processes (Theodosiou et al. 2019). For instance, Frisch et al. (2014) showed that the nutrient use efficiency of freshwater zooplankton can evolve in response to cultural eutrophication, but despite the relevance of eco-evolutionary dynamics, we still know little on how the metabolic nutritional demands of ectotherm primary consumers may shift in response to long-term exposure to different temperatures and resource qualities. Hence, long-term exposure experiments are needed to test if sensitivity to nutrient limitation is modulated by temperature, and whether it is counteracted by evolutionary responses (Table 1). Data from Laspoumaderes et al. (2022) indicate that the TER is not a constant value, but that it varies with temperature, with a maximum occurring at temperatures close to the consumers' thermal environment in nature. This may suggest that the maximum value of the TER reflects an adaptation of consumers to optimise their nutrient metabolism, thereby reducing their metabolic nutrient requirements and lowering the risk of nutrient limitation at ambient temperatures. Testing this hypothesis in long-term experiments shows great promise for advancing our understanding of the role eco-evolutionary processes play in driving the metabolic requirements of aquatic and terrestrial ectotherms (Table 1). These experiments would allow observing whether certain populations are more prone to instability under stress and generalising concepts that may apply across ecosystems.

### Trophodynamics

The health of ecosystems has been defined according to five criteria: 1) ability to maintain equilibrium within the system (i.e. internal stability), 2) diversity and complexity, 3) ability to cope with external disturbances (i.e. stability and resilience), 4) being a growing and developing system, and 5) balance between the compartments (i.e. evenness of energy and matter flows) (Jorgensen and Gobster 2010, Costanza 2012). Interestingly, these features are represented in the functioning of food webs, itself determined by the strength of interactions between coexisting populations. Interaction strength refers to the magnitude of the effect of one species on another. Because different species are directly and indirectly connected through a complex web of interactions, impacts that affect one population in the community can have ramifications for others through multiple pathways that may be of different sign or strength (Landi et al. 2018, Bartley et al. 2019). This is particularly true for communities characterised by a high connectance, which is the case for planktonic and insect food webs (Table 1). Hence, interaction strength is a promising descriptor of the extent to which the physical and chemical environment, and in particular nutrient and temperature conditions, play out through the ecosystem (Wrona et al. 2006). While the interest in interaction strength has been motivated by the consequences of species loss or addition, the influence of abiotic conditions has received less attention. However, by influencing the biomass and nutritional value of resources, temperature and nutrient conditions are likely to impact interactions within these

food webs (Wrona et al. 2006, Meddeb et al. 2018). More specifically, by modulating the metabolic requirements of ectotherm primary consumers, temperature drives their diet preferences (Boersma et al. 2016, Rho and Lee 2017) and the top-down pressure exerted on specific resources. We expect that such modulations of interaction strength may influence the dynamics and biomass of individual resources, and may ultimately destabilize food webs (Table 1). This is particularly true for interactions occurring at low trophic levels, as destabilizing processes can travel up the food web and tend to be exacerbated at higher trophic levels (McCann 2012). Hence, studies incorporating information on metabolic requirements and their influence on the feeding behaviour of omnivores are needed to assess food web stability.

## Concluding remarks

We propose that identifying overarching ecological rules that apply to freshwater, marine, and terrestrial systems has a strong potential to increase our knowledge on the environmental conditions driving food webs. For instance, quantifying nutritional mismatches between resource quality and the nutritional requirements of ectotherm consumers will increase our understanding of large scale changes such as biodiversity loss. Advances in Nutritional thermal ecology will also enable us to identify idiosyncrasies among biomes such as the potential influence of different degrees in temperature fluctuations, which are generally rapid and larger in terrestrial systems, and slower and weaker in freshwater and marine systems. It is important to consider that the different biomes also differ in the identity of the nutrient limiting primary production, with nitrogen typically being limiting in many marine and terrestrial systems and phosphorus in freshwater habitats (Elser et al. 2007). Since phosphorus is involved in energy transfer and nucleic acids while nitrogen is associated with protein activity, nutrient-specific physiological responses to temperature may differ between ectotherms consumers in various biomes. Furthermore, temperature modulations of organism nutrient requirements might have large implications for nutrient recycling in food webs, which in turn, qualitatively and quantitatively feeds back to the ectotherms' resource pool. Understanding these processes will enhance our ability to predict how food webs will be structured and function under changing temperature (global warming) and biogeochemical cycles.

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## Author contributions

**Cedric L. Meunier:** Conceptualization (lead); Investigation (lead); Methodology (lead); Project administration (lead); Supervision (lead); Validation (lead); Visualization (lead);

Writing – original draft (lead); Writing – review and editing (lead). **Inga V. Kirstein:** Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Validation (supporting); Writing – review and editing (equal). **Felix Weber:** Conceptualization (supporting); Investigation (supporting); Validation (supporting); Writing – review and editing (equal). **Ann Marielle Evarita:** Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Validation (supporting); Writing – review and editing (equal). **Cecilia Laspoumaderes:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal). **Maarten Boersma:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal).

## Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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